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COORDINATED PREY CAPTURE BY *NOVOMESSOR COCKERELLI* (HYMENOPTERA: FORMICIDAE)

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Abstract.—*Novomessor cockerelli* uses coordinated behavior to subdue large orthopteran prey. When a partially disabled grasshopper is encountered, the first worker finding it mounts the dorsum of the grasshopper and clamps its mandibles over the wings, thus preventing escape by flight. Workers which arrive subsequently systematically remove or subjugate additional appendages. Behavioral coordination allows *N. cockerelli* to efficiently exploit large orthopteran prey which would otherwise escape if workers attempted to capture these individually.

The genus *Novomessor* comprises three species. Of these, the species *N. cockerelli* (Andre) is encountered commonly in the intermountain plains of the deserts of southern North America (Wheeler and Creighton, 1934). Although the generic name suggests that *N. cockerelli* is a harvester ant, it is in fact omnivorous (Creighton, 1950; Chew, 1977; Whitford, 1978), and insects comprise about one-half of its normal forage (Whitford et al., 1980).

N. cockerelli normally employs an individual foraging strategy (Whitford, 1976; Davidson, 1977) but is also capable of recruiting and cooperatively carrying large food items (Hölldobler et al., 1978). Both chemical (Hölldobler et al., 1978) and vibrational (Markl and Hölldobler, 1978) signals are used during recruitment. Here we report on cooperative and coordinated prey capture by *N. cockerelli* under field conditions, paying particular attention to the adaptive sequences of behaviors by individual foragers.

METHODS AND MATERIALS

Studies were conducted at the Jornada Experimental Range, 60 km NNE of Las Cruces, New Mexico, from May to July, 1979. The site has been described in detail elsewhere (Whitford et al., 1980). All studies were performed from 0800–1100 hr (MDT) during weekly visits to the site to collect long-term data on related projects.

Two separate observational series were performed. In the first, grasshoppers were hand collected and placed in an active entrance to a *N. cockerelli* nest. The sequence of attack by workers of *N. cockerelli* on the body parts

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of the grasshopper were recorded, as well as the ability of the workers to subjugate and capture the grasshopper. The body parts sequenced were the wings, antennae, pro-, meso-, and metathoracic legs, the cervix of the head, and the abdomen. All of the latter six body regions were combined and compared with the sequence of attack on the wings, using the binomial test (Siegel, 1956). Likewise, the ability of the workers to capture the grasshopper was dichotomized: capture or escape.

In the second series of observations, grasshoppers were captured and tethered with a fine copper wire which was passed through the body from the pronotum to the mesosternum. The copper wire was then anchored by a stone. The length of the copper wire from grasshopper to anchor was approximately 10 cm, allowing the grasshopper to move but not to take flight. For each of five distances from the nest entrance (0.5, 1.0, 2.0, 4.0 and 6.0 m), 16 separate grasshoppers were tethered. The number of grasshoppers found at each distance upwind from the nest entrance per distance class, and the maximum number of *N. cockerelli* workers present at the grasshopper during the 30 min. period were recorded. The sequence of attack by workers on tethered grasshoppers was recorded as described previously. Only 45 of the 80 grasshoppers offered were attacked, and only data from these successful attacks are presented. The sequences of attack on the body parts were recorded in inverse order, i.e., 7 = attacked first, 1 = attacked last. The number of occurrences of attack observed for each sequence was multiplied by the rank for that sequence. By dividing this weighted sum by 315, or the expected weighted score if that body part was always attacked first, a relative preference for attack on each of the 7 body regions was obtained.

RESULTS AND DISCUSSION

A total of 53 grasshoppers were captured and placed at the nest entrances of active *N. cockerelli* nests. Of these 53, 39 (74%) escaped. Of the 36 grasshoppers offered by this technique which were attacked, the first worker attacking the grasshopper mounted the dorsum and clamped its mandibles over the wings in 28 (78%) of the observations, indicating a highly significant preference for attacking the wings (binomial test, $P < 0.001$, Siegel, 1956). Moreover, all 14 grasshoppers which were captured by *N. cockerelli* workers were first attacked by this method, as well as 14 of the 36 grasshoppers attacked which escaped. It should be noted that only about one-quarter (14/53) of grasshoppers presented at the entrances of active nests were captured.

The conditional probability of encounter and the maximum number of workers present at the immobilized grasshoppers declined slightly with increasing distance from the nest (Table 1). However, this reduction was not dramatic until a distance of 6.0 m was reached (Table 1). Hölldobler et al. (1978) have demonstrated that recruitment is mediated by poison gland

Table 1. The conditional probability of encounter and the maximum number of workers arriving at tethered grasshoppers at various distances from the entrance of *Novomessor cockerelli* nests.

Distance (m) from nest entrance	Conditional probability of encounter[1]	Number of workers arriving (mean ± 1 standard deviation)[2]
0.5	0.6875	24.6 ± 16.5
1.0	0.5000	22.6 ± 12.3
2.0	0.6250	19.8 ± 10.6
4.0	0.5625	15.2 ± 8.5
6.0	0.4375	6.0 ± 3.7

[1] The number of grasshoppers encountered within 30 min./16, the total number of grasshoppers offered at each distance.

[2] Calculated only for those grasshoppers which were encountered within 30 minutes.

secretions deposited by individual ants from the food source to the nest. The decline in the number of workers present at the food source (grasshoppers) was similar to the pattern reported by Hölldobler et al. (1978) to artificial food sources.

As in the first series of experiments, the first worker which attacked a tethered grasshopper mounted the dorsum and clamped its mandibles over the wings in 34 of the 45 attacks observed. Likewise, a significant preference for attacking the wings first was found (binomial test, $P < 0.0001$, Siegel, 1956). The metathoracic legs and the antennae were the body parts of the grasshopper attacked most frequently sooner than the other body parts after the wings (Table 2).

The sequence of prey capture employed by *N. cockerelli* is thus coordinated. Moreover, the sequence of attack is apparently very adaptive. By pinning the wings of orthopteran prey first, the prey is thus deprived of flight as an escape mechanism. Subsequent subjugation of the jumping legs and/or antennae then deprives the grasshopper of saltatorial escape, or flight, directed by the antennae, if the ant subjugating the wings is dislodged.

Given our results, it is uncertain how frequently *N. cockerelli* may employ this adaptive sequence of prey capture. Grasshoppers placed in the entrances of active nests were only captured about one-quarter of the times tested. It is unlikely that many grasshoppers would land at an active nest entrance. More likely, *N. cockerelli* probably employs the sequence described in capturing injured or weakened grasshoppers. Grasshoppers escaping bird strikes, or the attacks of lizards, scorpions or other desert predators may be injured to the extent that rapid escape is not possible. Under such conditions, *N. cockerelli,* employing the adaptive sequences of behavior described, may be able to capture these individuals.

Coordinated prey capture of orthopteran prey, organized around adaptive

Table 2. Observed frequency distribution of the order of attack on the body parts of immobilized grasshoppers by workers of *Novomessor cockerelli*.

Behavior/ body part	Observed order of attack 1	2	3	4	5	6	7	Totals	Score*
Pin wings	34	5	1	1	4	0	0	45	0.917
Grab/clip									
Antenna	2	10	11	5	16	0	1	45	0.679
Prothoracic leg	3	6	9	8	11	7	1	45	0.578
Mesothoracic leg	1	5	14	8	7	8	2	45	0.565
Metathoracic leg	4	14	8	15	3	1	0	45	0.708
Head (cervix)	0	0	2	5	3	16	19	45	0.286
Abdomen	1	5	0	3	1	13	22	45	0.282
Totals	45	45	45	45	45	45	45	315	

* Obtained by weighting each frequency (rank 1 = 7, rank 2 = 6, etc.) by multiplying the frequency by its rank and then dividing by the maximum possible score, 315 (i.e., all 45 observations given rank of 1, or 45 × 7).

sequences of behavior, and the consequential cooperative removal of captured prey to the nest (Hölldobler et al., 1978), is an efficient strategy of resource procurement, as well as a means of counteracting interference competition by mass-recruiting ant species. With the exception of army ants, termite predator specialists of the genus *Leptogenys*, and some of the slave-making formicines, we know of no instance of pack-like hunting behavior being recorded for ants. Indeed, the constancy of the attack sequences reported here is similar to that observed in pack-hunting felines and canines (Wilson, 1975).

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